

Food Searching and Exploitation by a Primary Consumer (*Ancylus fluviatilis*) in a Stochastic Environment: Nonrandom Movement Patterns

by

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With 4 figures

ABSTRACT

Periphyton layers on stony substrates are patchy food sources for alga-consuming herbivores in rivers and littoral zones of lakes. A possible strategy for such a consumer is a "random walk" with additional adaptive behavioural mechanisms to increase the chance of finding suitable patches. This hypothesis was investigated in *Ancylus fluviatilis* (Gastropoda — Basommatophora). Orientation and preferred feeding areas were studied, and interpreted on the basis of previous determinations of feeding rates. Foraging in this species seems to be a combination of "area restricting searching" and "giving up time" strategies, both being adaptive in this habitat.

INTRODUCTION

Consumers while foraging normally encounter nonrandom, clumped dispersion patterns of food items (WIENS 1976, GILL & WOLF 1977). One consequence of this stochastic dispersion of resources is the patchy distribution of the consumer population as well (ROUGHGARDEN 1977). A consumer's response to variation in prey density or quality can affect its foraging efficiency or its rate of net gain (TOWNSEND & HUGHES 1981). One possible strategy for the consumer is to detect the distribution and availability of food items by means of accurate sensory mechanisms. A "random walk" movement is an alternative strategy used, e.g., by marine intertidal limpets. Additional behavioural

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mechanisms are often found in connection with random walk strategies and probably improve overall consumption rates above those possible from pure random foraging (GILL & WOLF 1977). Both random walk and sensory detection strategies, to a certain degree at least, are often combined in gastropods with homing behaviour (FUNKE 1964, MACKAY & UNDERWOOD 1977, COOK 1979, KITTING 1980).

The European Basommatophoran snail *Ancylus fluviatilis* lives as a primary consumer of algae on the stony substrates of rivers and littoral zones of lakes. Its food source is patchily distributed. Many papers have dealt with quantitative aspects of feeding rates and energy metabolism in *Ancylus* (STREIT 1975 etc., CALOW 1975 etc.). Its patterns of foraging, however, have not so far been studied in detail, nor have they been related to either energetic considerations or optimal foraging theory. This paper attempts to provide such an analysis. It shows that certain aspects of movement in *Ancylus* are nonrandom.

MATERIALS AND METHODS

The limpets were all collected in a small river near Lake Constance. The methods used were the same as described formerly (STREIT 1975, 1978, STREIT *et al.* 1978), i.e. a combination of

- a) field studies,
- b) studies in experimental rearing channels of 6 m length each,
- c) small-scale experimental studies of feeding rates, metabolic efficiencies, and storage product determination, partly by use of ^{14}C labelled algal materials. Feeding experiments were mostly done by offering artificial periphyton on a millipore filter to the limpets. Carbon was measured by means of a C-H-analyzer system.

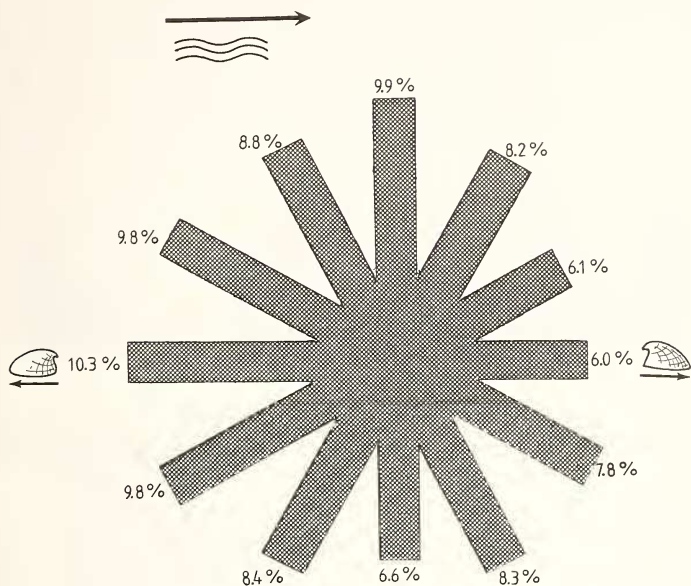
RESULTS

a) The effect of the water current on the orientation of limpets was studied using the rearing channel system. The temperatures in the two channels used for this study were 11°C and 15°C respectively. Differences in orientation between the two temperatures could not be detected. The current velocity was about 20 cm/s. A total of 207 individuals, all crawling on the top of the stones, were individually assigned to one of 12 sectors of 30°. The sector limits were chosen so that one limit lay exactly in the direction of the water flow. Adjacent sectors were then taken together and the arithmetic mean of each pair of sectors was finally plotted as a percentage of the total in Fig. 1a. The differences of the individual sector values to the expected mean sector value (8.33%) shows a significant relation to the angle between orientation and the water current (Fig. 1b). Thus, limpets within the population are orientated in all directions, but a weak but significant preference for the upstream direction is demonstrable.

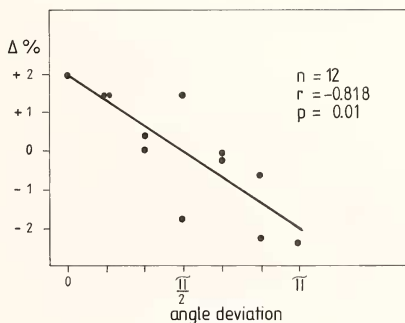
It is not known whether this orientation would become more pronounced at elevated current velocities. We also do not know whether the reaction observed is an individual adaptation to minimize the effect of water current, nor whether this tendency would compensate possible longterm downstream drift of the population by means of an overall upward movement.

b) Field studies suggested a relationship between ambient temperature and percent distribution of the limpets between the top of stones and the bottom. A long-term experimental study with varying temperatures between 2°C and 10°C exhibited the per-

FIG. 1.

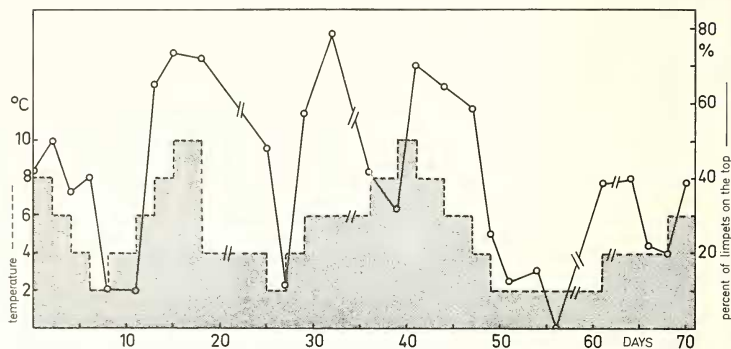


a) Orientation of *A. fluviatilis* according to water current. The percentage of limpets in each sector of $30^\circ (= \pi/6)$ is shown.

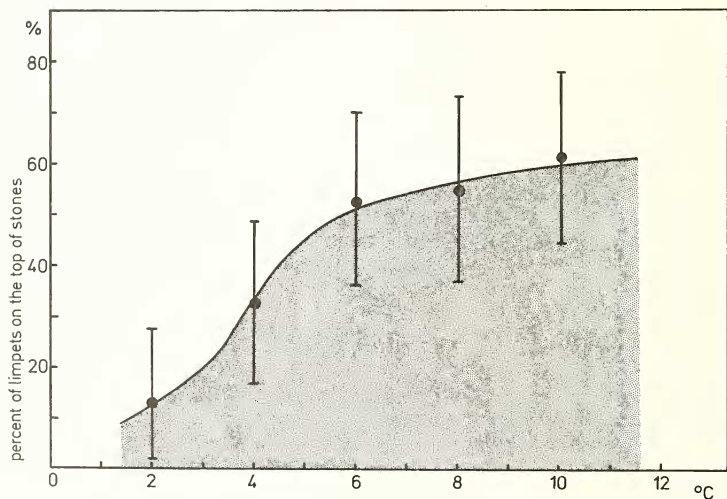


b) Deviation from the expected mean (8.33%) in relation to angle deviation from counter current direction.

FIG. 2.



- a) A long-term experimental study on dispersion pattern of *Ancylus fluviatilis* on stony substrates. Variation of ambient temperature between 2° C and 10° C. At the interruption points, some new limpets were introduced to replace those crawling on the glass wall. Experimental area: 30 × 20 cm.



- b) Correlation between ambient temperature and percentage of limpets on the top of stones. Bars indicate + - one standard deviation of individual measurements.

centages plotted in Fig. 2a. Only the percentages of distribution patterns are predictable (Fig. 2b). The individual limpet behaves in an unpredictable way. It was found that during the time that the limpets are at the bottom of the stones, they consume significantly less than during the time they are on the top. Intervals of resting, crawling, and feeding alternate in an irregular way, as was described earlier (STREIT 1977/78).

The adaptive value of this aspect of dispersion may be either or both of the following: First, it may be more adaptive to spend inactive periods at the bottom, which is always more sheltered than are the tops of stones. Secondly, the repeated retiring to the bottom may be the only way in which movement from one stone to the next is automatically achieved.

c) Crawling periods without feeding are longer and commoner if unsuitable concentrations of periphyton are encountered. Only algal layers of a defined thickness are accepted for food. For an experimental series of studies with the diatom *Nitzschia actinastroides*, the limits of acceptance were about $0.1\text{--}0.2 \mu\text{g C/mm}^2$ at the lower limit and about $2 \mu\text{g C/mm}^2$ at the upper. Below about $0.3\text{--}0.4 \mu\text{g C/mm}^2$, the amount ingested per unit time would not allow a long-term positive carbon balance (Fig. 3).

The carbon content of natural periphyton in the habitat of the limpets was determined by scraping with a blade areas of about $1\text{--}2 \text{ cm}^2$ on stones at different sites where

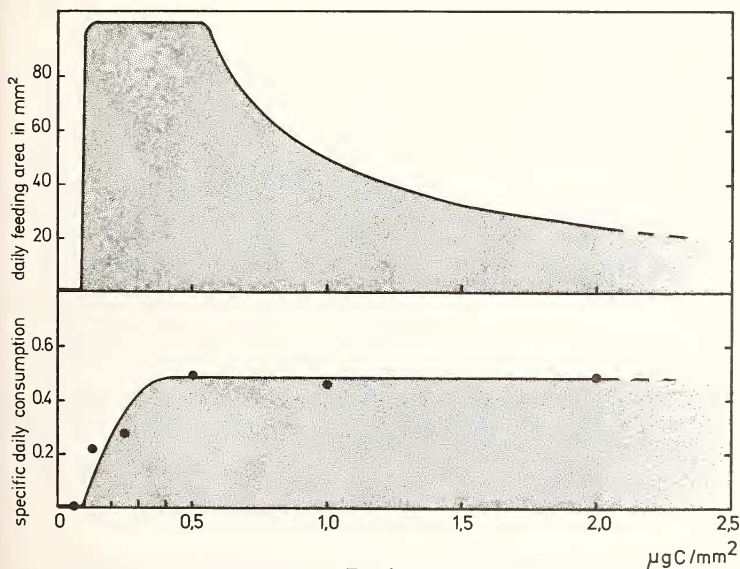


FIG. 3.

Specific daily consumption rates (below) and daily feeding area in mm^2 (slightly idealized, above), of *Nitzschia actinastroides* (Diatomeae) in relation to carbon content of the algal layer. Mean values of series of determinations are indicated.

limpets were found. These samples showed relatively rich or relatively poor algal layers in different rivers. But suitable concentration patches (i.e., between 0.4 and 2 $\mu\text{g C/mm}^2$) could be found in all habitats, though pronounced differences in different seasons could be detected (Fig. 4).

d) Another nonrandom activity is selection of oviposition sites. Egg capsules, containing between 1-10 eggs (mostly about 4-5) are stuck at the edge of stones near the bottom. The newly hatched juveniles are not very mobile and are found near the original oviposition site during the first days or weeks. It is there that they consume food. These patches often have thinner algal layers and thus are more suitable places for the juveniles, as the juvenile teeth are smaller than the adult ones (STREIT 1975). The potential for intraspecific competition between juveniles and adults is thus lowered.

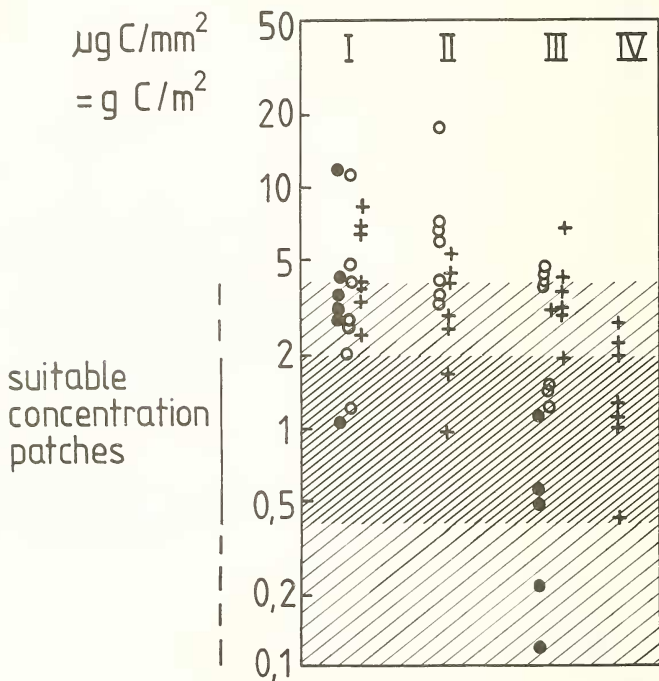


FIG. 4.

60 algal patches on natural habitats of *A. fluviatilis*, as determined by scraping areas of 1-2 cm^2 with a blade. I-IV are different river habitats near Lake Constance (cf. STREIT 1975). Sampling dates were: ● July 27, 1977; ○ November 2, 1977; + February 2, 1978. About 25% of the patches exhibited suitable concentration patches, 42% most probably unsuitable patches, 33% definitely unsuitable patches.

e) Related to the snail's alternating periods of feeding and crawling, a mobile lipid storage compartment is found within the limpet, and especially in the midgut gland. It enables the limpet to be active for up to several days without feeding and to move distances of up to about one meter from the original starting point. The duration of the reserve will be determined by the ambient temperature and by the general activity of the animal. "Extensive feeding" (SCHWENK & SCHWOERBEL 1973) is also seen, i.e., feeding is observed during crawling phases. An additional carbohydrate storage compartment is distributed more equally throughout the body and probably is connected primarily with egg laying. This storage compartment is protected until lipid reserves are exhausted (STREIT 1978). As a consequence, egg laying can occur even in starving animals (i.e., animals with empty lipid reserves), though egg numbers then will decrease (STREIT 1975). This seems to be an additional mechanism by which a more equal distribution of egg capsules over the stony bottom of the river can be achieved.

GENERAL DISCUSSION

When the food distribution is clumped, a consumer should move in ways that keep it in a food clump and that move it rapidly between clumps. This may be accomplished by turning more and moving shorter distances when a clump is encountered than when it is not encountered. Such behaviour in connection with food searching and exploitation is well documented for a variety of organisms, as for example in birds (TINBERGEN *et al.* 1967, CHARNOV, *et al.* 1976, SMITH 1974, GILL & WOLF 1977).

In areas of suitable food concentrations, the limpets tend to stay for a longer period than in other areas, but none the less leave the place after some time. Thus the foraging rules of this species seem to be a combination of "area restricting searching" and "giving up time" strategy (GILL & WOLF 1977).

In marine limpets, even unusually high experimental densities of limpets failed to decrease algal abundancies detectably. Algal declines were attributed to physical factors (KITTING 1980). Though overall estimations of the effect of grazing of *A. fluviatilis* on the algal layer in the natural habitat are lacking, a local "grazing effect" in the patchy environment of the limpets seems to be highly probable and has been proven to occur in experimental systems. The recory of periphyton in running water was determined e.g., by MCMAHON *et al.* (1974). Standing crop biomass of periphyton growing on microscope slides needed at least about a month to attain a value of $0.1 \mu\text{g C/mm}^2$. The C:N ratio, however, was rather favourable with values of 2-10. CATTANEO & GHITTORI (1975) found values of about $1 \mu\text{g C/mm}^2$ within about 1 week in a Ticino river and C:N ratios of about 6-8. At any case, revisiting the same patch within less than 1 week would be inappropriate for the limpets. The "giving up time" strategy seems to be appropriate under these circumstances and leads the limpets to adjacent stones with possibly suitable patches. Orientation to the water current is thus of little importance, and accordingly is only demonstrable by statistical analysis.

ZUSAMMENFASSUNG

Aufwuchs konsumierende Primärkonsumenten des steinigen Litorals unserer Fließgewässer und Seen treffen geeignete Nahrungsquellen als lokal gehäufte, zufällig auf dem Substrat verstreute Bezirke. Eine mögliche Strategie für den Konsumenten ist ein „Random walk“-Bewegungsverhalten, dem zusätzliche adaptive Verhaltensmechanismen

aufgelagert sind, die seine Chance erhöhen, geeignete Nahrungsquellen zu finden. Diese Hypothese wurde an der Flussmützenschnecke *Ancylus fluviatilis* (Gastropoda-Basommatophora) getestet.

Zunächst wurde getestet, ob rheotaktische Komponenten eine Rolle für die Wanderung spielen. Die Analyse in einer künstlichen Fließwasserrinne zeigte, dass die Schnecken in alle Richtungen orientiert sind, dass aber doch eine statistisch nachweisbare schwache Bevorzugung der Gegenströmungsrichtung vorhanden ist (Fig. 1).

Unter- und Oberseite der Steine sind von sehr unterschiedlicher Bedeutung für die Schnecken. Oben (und auch an den Seiten) sind günstigere Nahrungsbedingungen zu finden, als an der Unterseite, doch sind die Schnecken hier vielleicht geschützter. Vor allem aber ist nur über die Unterseite ein Übergang zwischen den Steinen möglich. Die Schnecken wechseln spontan und im Einzelfall nicht vorhersehbar zwischen „oben“ und „unten“, doch ist der statistische Prozentsatz der Verteilung temperaturabhängig und deterministisch vorhersagbar (Fig. 2).

Lokale Bezirke („patches“) mit zu geringer Algendichte werden nicht beweidet. Sie werden aber ab einer Dichte von ca. $0.1\text{--}0.2\ \mu\text{g C/mm}^2$ (nach Experimenten mit der Diatomee *Nitzschia actinastroides*) akzeptiert. Über etwa $2\ \mu\text{g C/mm}^2$ wirkt die Funktionsweise des Radulaapparates limitierend auf das erfolgreiche Abkratzen der Algen vom Untergrund (Fig. 3).

Freilandmessungen der Algendichte zeigten, dass in jedem Bachsystem, in dem die Schnecke gefunden wurde, viele zusagende Nahrungs- „patches“ zu finden sind, doch — je nach Jahreszeit — auch unterschiedlich viele nicht-zusagende (Fig. 4). Die schon früher beschriebenen Befunde über das Verharren an Nahrungsquellen („area restricting searching“) bei trotzdem spontan auftretenden neuen „walks“ („giving up time strategy“) werden als adaptive Einrichtungen zum Auffinden gerade solcher „stochastisch“ verteilter Nahrungsquellen gesehen.

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